RE-EVALUATION OF CUPRESSACEAE AND TAXODIACEAE: A PROPOSED MERGER

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Among the many interesting coniferous trees, those referred to Taxodiaceae and Cupressaceae are particularly noteworthy to both botanists and laymen. Foremost among these are such restricted endemics as the taxodiaceous coast redwood (*Sequoia sempervirens*) and bigtree (*Sequoiadendron giganteum*), but species of the cupressaceous genera *Cupressus, Juniperus, Thuja, Chamaecyparis,* and *Calocedrus* have also been frequently discussed. Familial classification of these and other conifers has seemed an unlikely source of controversy since Pilger (1926) decisively split the classical Pinaceae (Abietineae) into seven families: Taxaceae, Podocarpaceae, Araucariaceae, Cephalotaxaceae, Pinaceae s. s., Taxodiaceae, and Cupressaceae. Florin (1948) discussed the reproductive morphology of the taxads and concluded that they should be segregated from Pilger's other families in a separate order Taxales. In line with his suggestion they are omitted from discussion here. Pilger's delimitations of the other families have remained virtually unchallenged by taxonomists, who have concentrated instead on many perplexing problems at other taxonomic levels (Florin, 1955; Janchen, 1950). The six-family scheme has also served as the framework for presentation of results of virtually all modern reviews of such aspects of conifers as epidermal characters (Florin, 1931), external leaf morphology (de Laubenfels, 1953), wood anatomy (Greguss, 1955; 1972), shoot apex (Johnson, 1951), chromosome number (Khoshoo, 1961), male gametophyte (Sterling, 1963), female gametophyte (Maheshwari and Singh, 1967), embryogeny (Doyle, 1963; Doyle and Brennan, 1971; 1972; Roy Chowdhury, 1962), pollination (Doyle, 1945b), structure of megasporangiate strobilus (Florin, 1951), phytochemistry (Hegnauer, 1962), and geographical distribution (Buchhold, 1948; Florin, 1963; Li, 1953b).

Circumscriptions of the families segregated by Pilger and accepted by subsequent authors are based on a number of vegetative and reproductive characters, but primary distinctions are derived from the structure of their megasporangiate strobili (Pilger, 1926; Sporne, 1965). All are separable on this basis except Cupressaceae and Taxodiaceae, which show fundamental similarities in development and final form of the ovuliferous scale-bract complexes (Florin, 1951). These two families, in contrast to all other pairs of conifer families, are usually distinguished only by leaf form and phyllotaxis. Most modern authors have

recognized a close relationship between these two families but have kept them separate (Takhtajan, 1953).

I have come to believe that the genera usually assigned to Cupressaceae and Taxodiaceae should be assigned to one family, which must, for reasons of priority, be called Cupressaceae. Two lines of evidence are fundamental to this proposition. Both groups of genera taken together show the same degree of morphological cohesiveness as other single conifer families. As a group they share a distinctive array of vegetative and reproductive characters that separate them from the equally distinctive Podocarpaceae, Araucariaceae, Cephalotaxaceae, and Pinaceae. Furthermore, *Sequoia* and its allies are as closely related to *Cupressus* (which is similar to the probable ancestor of many northern hemisphere cupressaceous genera) as they are to other genera usually included with them in a segregate family. They are likewise related to *Callitris* and other southern hemisphere cupressaceous genera. The latter are less closely allied to *Cupressus* than are their northern hemisphere counterparts and probably represent two or three lineages coordinate with the *Cupressus*-line and linked to it by a common taxodiaceous ancestor.

The group of twenty-eight genera in question has a wide geographical distribution in temperate regions (Table 1), comparable to those of the other large conifer families, Pinaceae and Podocarpaceae, though more bihemispheric than either of these (Florin, 1963). While most modern systematists have accepted segregation of these genera into two families, agreement on this arrangement is relatively recent and older treatments often group them along rather different lines. Linnaeus (1753) described *Taxodium distichum,* the only taxodiaceous tree known to him, as a species of *Cupressus,* just as Poiret (1817) subsequently first described *Glyptostrobus lineatus* as a species of *Thuja.* Similarities among some genera are also reflected in such specific epithets as "cupressoides" (*Athrotaxis, Fitzroya, Widdringtonia*), "glyptostroboides" (*Metasequoia*), "cryptomerioides" (*Taiwania*), and "thyoides" (*Chamaecyparis*).

Families recognized by early students of the Coniferales often had quite different circumscriptions than those accepted by Pilger (1926). Endlicher (1847) placed all conifers in four families (for convenience I use the term family for the taxonomic grouping generally called order or *ordo naturalis* by nineteenth century botanists) and included in two of them all genera here referred to Cupressaceae s. l. Endlicher's Cupressineae comprised all cupressaceous genera as well as *Taxodium, Glyptostrobus,* and *Cryptomeria,* while other taxodiaceous genera were included with *Agathis* (Araucariaceae) in a tribe of his Abietineae. Gordon (1880), in contrast, recognized only two families of conifers. Cupressaceous and taxodiaceous genera are found in all three tribes of his Pinaceae. Most of these genera constituted his tribe Cupresseae, while *Juniperus* was placed in a monotypic tribe and *Cunninghamia, Athrotaxis,* and *Sciadopitys* together formed a "section" included in his

tribe Abietineae along with "sections" for the araucarians and abieti-
neans. Other variations are displayed in important taxonomic systems
of Gordon (1858), Carrière (1867), Parlatore (1868), Masters (1893),
and Vierhapper (1910). Most commonly in these and other systems the

TABLE 1. NEW ARRANGEMENT OF CUPRESSACEAE BARTLING, 1830 (INCL. TAXO-
DIACEAE WARMING, 1884). Column a: genera formerly assigned to Taxodiaceae (T)
or to Cupressaceae (C). Column b: number of species. Column c: generalized
distribution.

	a	b	c
Subfamily Sciadopitoideae Saxton, 1913			
Sciadopitys Siebold & Zuccarini, 1842	T	1	Japan
Subfamily Cupressoideae K. Koch, 1873			
Tribe Cupresseae Dumortier, 1827			
Subtribe 1			
Sequoia Endlicher, 1847	T	1	Calif.
Sequoiadendron Buchholz, 1939	T	1	Calif.
Subtribe 2			
Metasequoia Hu & Cheng, 1948	T	1	China
Subtribe 3			
Cupressus Linnaeus, 1753	C	ca 15	N.Hemis.
Chamaecyparis Spach, 1842	C	6	N.Hemis.
Fokienia A. Henry & Thomas, 1911	C	2	China
Platycladus Spach, 1842 (= *Biota* Endlicher, 1847)	C	1	China
Thujopsis Siebold & Zuccarini, 1842	C	1	Japan
Thuja Linnaeus, 1753	C	5	N.Hemis.
Microbiota Komarov, 1923	C	1	Siberia
Calocedrus Kurz, 1873			
(= *Heyderia* K. Koch, 1873)	C	3	N.Pac.
Juniperus Linnaeus, 1753 (incl. *Arceuthos* Antoine &			
Kotschy, 1854)	C	ca 60	N.Hemis.
Subtribe 4			
Callitris Ventenat, 1808 (incl. *Octoclinis* F. v.			
Mueller, 1857)	C	16	Austr.
Actinostrobus Miquel, 1845	C	3	Austr.
Neocallitropsis Florin, 1931	C	1	N. Caled.
Fitzroya J. D. Hooker, 1851	C	1	Chile
Diselma J. D. Hooker, 1857	C	1	Tasm.
Widdringtonia Endlicher, 1847	C	3	S.Afr.
Tetraclinis Masters, 1892	C	1	N.Afr.
Libocedrus Endlicher, 1847 (incl. *Papuacedrus* Li, 1953;			
Pilgerodendron Florin, 1930)	C	9	S.Pac.
Austrocedrus Florin & Boutelje, 1954	C	1	Chile
Subtribe 5			
Taxodium Richard, 1810	T	2	N.Amer.
Glyptostrobus Endlicher, 1847	T	1	China
Tribe Cryptomerieae Vierhapper, 1910			
Cryptomeria D. Don, 1841	T	1	E.Asia
Tribe Cunninghamieae Zuccarini, 1842			
Subtribe 1			
Cunninghamia R. Brown, 1826	T	2	China
Taiwania Hayata, 1906	T	1	China
Subtribe 2			
Athrotaxis D. Don, 1841	T	3	Tasm.

group of cupressaceous genera, with or without addition of some taxodiaceous genera, forms a taxon coordinate with a second taxon comprising araucarians, abietineans, and some or all taxodiaceous genera.

The great surge of interest in gymnosperms at the turn of the twentieth century resulted in investigations of the life histories of several genera. Many of these investigations were accompanied by phylogenetic speculations, and Saxton (1913) went so far as to base his classification entirely on characters of gametophyte and embryogeny, which, a priori, he considered most important. Virtually alone among twentieth century authors, he considered separation of taxodiaceous and cupressaceous genera on the basis of phyllotaxis untenable and included them in a single family Cupressaceae, with rather different subgroupings than those proposed here (Table 1). His taxonomic system has been ignored by later workers, probably as a result of his extreme insistence on the unreliability of external characters. Lotsy (1911), in contrast, partially using the same evidence, divided conifers into two fundamentally divergent lines, placed the cupressaceous genera in his "Florales", and divided the taxodiaceous genera about equally between "Florales" and "Inflorescentiales" on the basis of degree of reduction of gametophytes. Much later, on the basis of wood characters, Greguss (1955) also segregated taxodiaceous and cupressaceous genera into widely separated groups. Neither of these attempts to recognize fundamental higher order differences between taxodiaceous and cupressaceous genera on the basis of restricted criteria has had any more acceptance than Saxton's emphasis on characteristics of gametophytes and embryogeny.

Besides segregating these genera into widely separated taxa Lotsy (1911) also treated them as representatives of five rather than the usual two families [Sequoiaceae, Cupressaceae, Actinostrobaceae, Juniperaceae, and Taxodineen (sic)]. Familial segregation culminated in the work of Hayata (1931, 1932). In addition to the families recognized, but not formally described, by Lotsy, Hayata proposed six additional segregates, Sciadopityaceae, Limnopityaceae (an alternative name for Taxodiaceae, restricted by him to *Taxodium* and *Glyptostrobus*), Cryptomeriaceae, Taiwaniaceae, Cunninghamiaceae, and Tetraclinaceae. Of these segregates, only Sciadopityaceae, restricted to the distinctive Japanese umbrella pine (*Sciadopitys verticillata*), has achieved occasional acceptance by subsequent authors. While most conifer taxonomists have been unwilling to accept numerous segregate families from among the taxodiaceous and cupressaceous genera, as late as 1948 Hu and Cheng assigned the newly discovered *Metasequoia glyptostroboides* to a monotypic Metasequoiaceae because its decussate phyllotaxis bridged the traditional gap between taxodiaceous and cupressaceous genera. Later authors have recognized *Metasequoia* as an unquestionably taxodiaceous genus, but Hu's and Cheng's contention of morphological intermediacy cannot be lightly dismissed.

Another factor contributing to continued recognition of separate families for taxodiaceous and cupressaceous genera has been a general trend toward generic segregation among conifers. This proliferation has been most notable in Podocarpaceae, where the large genus *Podocarpus* has recently been divided into several genera along old sectional lines (de Laubenfels, 1969; 1972) and in Cupressaceae s. s., with the fragmentation of *Libocedrus* (Florin, 1930; Florin and Boutelje, 1954; Kurz, 1873; Li, 1953a) and other genera. Among taxodiaceous genera, which comprise only fourteen species, this trend has been much less marked, and in this century only one segregate genus (*Sequoiadendron*) has been proposed for a previously known species (Buchholz, 1939). In contrast to the general acceptance of narrow generic concepts for cupressaceous genera, the validity of generic segregation of the redwoods was a subject of keen debate (Dayton, 1943; Doyle, 1945a), and even *Metasequoia* has been merged with *Sequoia* (Schwarz and Weide, 1962). The large number of cupressaceous genera often recognized has contributed to resistance to their merger in a single family with the smaller number of morphologically more diverse taxodiaceous genera. Generic multiplication has also resulted in hierarchical inflation for groupings of cupressaceous genera, as in Li's (1953a) classification, which distributes these genera among six tribes in two subfamilies, while Hida (1962) accepted only four suprageneric groups of taxodiaceous genera.

These diverse treatments of a group of genera currently recognized as being closely allied are not simply a result of ignorance on the part of our predecessors but are also a result of the complicated and rather obscure pattern of relationships displayed by relictual groups. Taxodiaceous genera are usually regarded as such a group of scattered Tertiary relicts, devoid of progressive elements, while Cupressaceae s. s., like Pinaceae and Podocarpaceae, is viewed as a more vigorous and successful group (de Laubenfels, 1965). The familial realignment proposed here (Table 1) suggests that cupressaceous genera are, in fact, the otherwise missing progressive elements of "Taxodiaceae" that have resisted Neogene climatic desiccation by adoption of scale leaves.

MATERIALS AND METHODS

I have approached the two parts of this study, comparisons of taxa at familial and generic levels, with the same set of methods. In a study at these levels, genetic evidence of relationship is lacking and the best available measure of relatedness is overall similarity of features between two taxa. One factor that has inhibited past discussion of relationships among conifers is the wide scattering of published comparative data. I have assembled here distributions of character states for all characters for which I could obtain comparable data for Pilger's six conifer families (Tables 2 and 3) and for all taxodiaceous genera as well as *Callitris* and

1. Phyllotaxis: 1. spiral, 2. opposite, 3. whorled, 4. spirals of opposite pairs. **2.** Ontogenetic sequence of leaf types: 1. flattened linear ➤ quadrangular ➤ quadrangular, 2. flattened linear ➤ flattened linear or scale ➤ flattened linear or scale, 3. flattened linear ➤ quadrangular ➤ multiveined, 4. scale ➤ flattened linear ➤ flattened linear, 5. scale ➤ multiveined ➤ multiveined. **3.** Mature leaf form: 1. agathoid, 2. taxoid, 3. cupressoid, 4. cryptomeroid, 5. pinoid. **4.** Unit of foliar dehiscence: 1. lateral shoot systems, 2. individual leaves. **5.** Haploid chromosome number: 9–13, 15, 17–19. **6.** Mycorrhizal association: 1. endotrophic, 2. ectotrophic, 3. nodular. **7.** Branching: 1. verticillate, 2. L-shaped, 3. ascending. **8.** Bark: 1. smooth, 2. fibrous, 3. plates. **9.** Crossfield pitting in secondary xylem: 1. podocarpoid, 2. dacrydioid, 3. araucarioid, 4. cupressoid, 5. piceoid, 6. taxodioid, 7. pinoid, 8. glyptostroboid..

10. Tangential wall of ray parenchyma cells in secondary xylem: 1. smooth, 2. sievelike, 3. scalariform. **11.** Resin ducts in secondary xylem: 1. absent, 2. present. **12.** Ray tracheids in secondary xylem: 1. absent, 2. present. **13.** Biflavonoid series: 1. amentoflavone, 2. hinokiflavone, 3. cupressuflavone, 4. agathisflavone, 5. dihydrobiflavonoids, 6. none. **14.** Cyclitols: 1. sequoyitol, 2. pinitol. **15.** Sieveelement plastids: 1. starch-containing, 2. starch- and protein-containing. **16.** Estolide wax: 1. absent, 2. present. **17.** Arrangement of microsporangiate strobili: 1. solitary, 2. spicate, 3. otherwise grouped. **18.** Position of microsporangiate strobili on shoot system: 1. lateral, 2. terminal. **19.** Orientation of microsporangia on microsporophyll: 1. appressed, 2. projecting, 3. pendent.

20. Number of microsporangia per microsporophyll: 2–15. **21.** Pollen form: 1. saccate, 2. spheroidal. **22.** Pollen aperture: 1. analept, 2. atreme, 3. microlept, 4. papillate leptoma. **23.** Development of male gametophyte: 1. araucarian, 2. taxodian, 3. abietinean. **24.** Division of generative cell in male gametophyte: 1. anticlinal, 2. periclinal, 3. periclinal inverted, 4. divides within pollen tubes. **25.** Male gametes: 1. equal, 2. unequal. **26.** Degree of fusion of ovuliferous scale with bract: 1. completely free, 2. nearly free, 3. considerably fused, 4. completely fused. **27.** Number of ovules per ovuliferous scale: 1–20. **28.** Ovule orientation: 1. erect, 2. inverted. **29.** Texture of ovuliferous scale: 1. woody, 2. fleshy.

30. Number of seed wings: 0–3. **31.** Seed storage product: 1. starch, 2. lipid. **32.** Grouping of archegonia in female gametophyte: 1. solitary, 2. in a ring, 3. in complexes. **33.** Position of archegonia: 1. micropylar, 2. lateral. **34.** Number of neck cells of archegonium: 2–15. **35.** Number of tiers of neck cells: 1–4. **36.** Ventral canal cell of archegonium: 1. absent or ephemeral, 2. present. **37.** Archegonial jacket: 1. absent or weakly developed, 2. well developed, 3. common to several archegonia. **38.** Number of free nuclear divisions of proembryo: 0–6. **39.** Number of cell tiers in proembryo before suspensor elongation: 2 (central mass with peripheral jacket)–4.

40. Equality of proembryonal tiers: 1. equal, 2. unequal. **41.** Types of embryonic suspensor: 1. prosuspensor, 2. primary suspensor, 3. secondary suspensor, 4. upper jacket cells. **42.** Embryonic cap: 1. absent, 2. lower jacket cells, 3. 1–2 cells. **43.** Accessory embryos: 1. absent, 2. above prosuspensor tier, 3. prosuspensor tier, 4. rosette or primary suspensor tiers, 5. embryonic. **44.** Cleavage polyembryony: 1. absent, 2. present. **45.** Number of cotyledons: 2–18. **46.** Number of vascular traces in cotyledons: 1–2.

Cupressus (taken respectively as generalized representatives of the southern and northern hemisphere cupressaceous lines; Tables 5 and 6). This information has come primarily from reviews cited in the first paragraph of this paper, supplemented by additional published accounts

TABLE 3. CHARACTERISTICS OF CONIFER FAMILIES USING CHARACTERS AND THEIR STATES AS LISTED IN TABLE 2. This table was compiled using the following references in addition to personal observations: Behnke (1974), de Laubenfels (1953; 1962), G. Erdtman (1957; 1965), Greguss (1955), Hegnauer (1962), Khoshoo (1961), Kindl and Hoffmann-Ostenhof (1966), Locksley (1973), Maheshwari and Singh (1967), Roy Chowdhury (1962), Sporne (1965), Sterling (1963). Character states in parentheses are rare in a family, often confined to a single genus.

PODOCARPACEAE: 1:1,2; 2:1,2; 3:1–4; 4:1; 5:9–13,15,17–19; 6:1; 7:1,3; 8:1,2; 9:1,2; 10:1; 11:1; 12:1; 13:1,(2); 14:1; 15:1; 16:1; 17:1,2; 18:1,2; 19:1; 20:2; 21:1; 22:1; 23:1; 24:1; 25:1,2; 26:1–4; 27:1; 28:1,2; 29:(1),2; 30:0; 31:1; 32:1,(3); 33:1; 34:4–15; 35:1; 36:2; 37:2; 38:4–5; 39:3; 40:2; 41:1,3; 42:3; 43:2; 44:1,2; 45:2; 46:2.

ARAUCARIACEAE: 1:1,2,4; 2:3,5; 3:1,2,4; 4:1; 5:13; 6:3; 7:1; 8:1; 9:3; 10:1; 11:1; 12:1; 13:1–4; 14:1; 15:1; 16:?; 17:1; 18:1,2; 19:2; 20:5–15; 21:2; 22:1,2; 23:1; 24:1; 25:1; 26:4; 27:1; 28:2; 29:1; 30:0,2; 31:1; 32:2; 33:1; 34:12; 35:1; 36:1; 37:2; 38:5–6; 39:2; 40:2; 41:3,4; 42:2; 43:1; 44:1; 45:2,4; 46:1,2.

CEPHALOTAXACEAE: 1:4; 2:4; 3:2; 4:1; 5:12; 6:2; 7:1; 8:2; 9:4; 10:1,(2); 11:1; 12:1; 13:1; 14:1,2; 15:1; 16:1; 17:2; 18:1; 19:3; 20:2,3; 21:2; 22:3,4; 23:2; 24:1; 25:2; 26:1; 27:2; 28:1; 29:2; 30:0; 31:1,2; 32:1; 33:1; 34:2–5; 35:1; 36:1; 37:1; 38:4; 39:3; 40:2; 41:1,3; 42:3; 43:3; 44:1; 45:2; 46:2.

PINACEAE: 1:1,(3); 2:1,2; 3:5; 4:(1),2; 5:12,(13); 6:2; 7:1,(2); 8:3; 9:5–7; 10:(1),2,(3); 11:1,2; 12:1,2; 13:6; 14:1,2; 15:2; 16:2; 17:1,2; 18:1,2; 19:1; 20:2; 21:1,2; 22:1; 23:3; 24:2; 25:2; 26:2; 27:2; 28:2; 29:1; 30:1; 31:2; 32:1; 33:1; 34:4–8; 35:2–4; 36:2; 37:2; 38:3; 39:4; 40:1; 41:2,3; 42:1; 43:4; 44:1,2; 45:3–18; 46:1,2.

"TAXODIACEAE": 1:1–(3); 2:1,2; 3:2–5; 4:1,(2); 5:(10),11; 6:2; 7:1,2; 8:2; 9:4,6,8; 10:1,2; 11:1,(2); 12:1,2; 13:1,2,5; 14:1,2; 15:1; 16:1,2; 17:1–3; 18:1,2; 19:2,3; 20:2–9; 21:2; 22:3,4; 23:2; 24:1–4; 25:1; 26:3,4; 27:2–9; 28:1,2; 29:1; 30:0–3; 31:2; 32:1–3; 33:1,2; 34:2–4; 35:1; 36:2; 37:1–3; 38:0–5; 39:3–4; 40:1,2; 41:1–3; 42:1; 43:2,5; 44:1,2; 45:2–6; 46:2.

CUPRESSACEAE S. S.: 1:(1)–3; 2:2; 3:3,4; 4:1; 5:11; 6:2; 7:1,2; 8:2; 9:4,6; 10:1–3; 11:1; 12:1,2; 13:1–(3); 14:1,2; 15:1; 16:2; 17:1; 18:2; 19:3; 20:(2)–6; 21:2; 22:3,4; 23:2; 24:2; 25:1; 26:4; 27:(1–2)–20; 28:1; 29:1,(2); 30:0–3; 31:2; 32:3; 33:1,2; 34:4; 35:1; 36:2; 37:2,3; 38:2–3; 39:3; 40:1,2; 41:1–3; 42:1; 43:5; 44:2; 45:2–4; 46:2.

(cited in Tables 3 and 6), and by examination of herbarium specimens in UC and of living plants in the collections cited in Acknowledgments. Further supplementary information was gathered during visits to natural populations of all genera of Cupressaceae s. l. native to North America, and in the course of an unpublished investigation of flavonoid constituents of all taxodiaceous genera and several cupressaceous genera (including *Cupressus*) conducted at Reed College, Portland, Oregon. The data were initially assembled in two descriptive charts (one for families and one for genera) arranged as character by taxon matrices. These charts were adapted for publication by assigning numbers to each character and character state (Tables 2 and 5) and then using these numbers in constructing character profiles for each family (Table 3) or genus (Table 6). Using the original data matrices, I tallied all similarities and differences for each pair of families and genera. I then divided similarities within each pair by the total number of similarities and dissimilarities between their constituents and multiplied by 100 to

obtain percent similarity values for pairs of families (Table 4) and genera (Table 7). The total number of comparisons for a pair is usually greater than the number of characters listed (Tables 2 and 5) because most families and genera display multiple or continuous character states for at least some characters. While not all characters are equally reflective of degree of relationship between taxa, the use of a wide array of characters helps to bypass any bias that might be introduced by equal weighting of a few characters. The likelihood of spurious indications of close relationship (as measured by high similarity values) resulting from convergence or coincidence decreases markedly with inclusion of increasing number of phases of the biology of the taxa involved (Sneath and Sokal, 1973).

The new classification of Cupressaceae s. l. proposed here (Table 1) is based primarily on the traditional criteria of morphology and development of megasporangiate strobili. On the whole, this complex of characters has provided a satisfactory and stable basis for classification of conifers. These features have been supplemented by indications from many of the other characters examined here, including vegetative characters. I consider the tribal groups rather definite, though *Athrotaxis* might perhaps be transferred to a monotypic tribe. These tribes are nearly equivalent to the subfamilies of Hida (1962) with the addition of cupressaceous genera. I am less certain of arrangement of genera within Cupresseae, which is by far the largest tribe with 4/5 of the genera in the family. Until lineages of cupressaceous genera are better understood, it seems wise to avoid formal nomenclatural recognition of the subtribal groups proposed here. Legitimate names are available for all other suprageneric groups I recognize (Table 1). For convenience, I refer throughout this paper to taxodiaceous and cupressaceous genera, terms that do not refer to taxonomically equivalent groups of genera but rather to the usual assignment of these genera to families.

Familial Characteristics

Similarity Values. Examination of a range of characters, taken from all phases of the conifer life cycle (Table 2), shows close overall agreement in these features (including such superficial characteristics as bark form and branching pattern, as well as the traditionally more

Table 4. Percentage Similarities of Conifer Families. Coefficients were calculated by dividing similarities by total number of comparisons (in parentheses) for each pair.

Podocarpaceae					
59(59)	Araucariaceae				
59(51)	40(53)	Cephalotaxaceae			
46(56)	31(58)	29(58)	Pinaceae		
52(77)	42(77)	45(74)	47(79)	"Taxodiaceae"	
46(63)	36(64)	41(59)	42(65)	90(73)	Cupressaceae s. s.

TABLE 5. LIST OF CHARACTERS AND CHARACTER STATES OF CUPRESSUS, CALLITRIS,
AND TAXODIACEOUS GENRA.

1. Mature phyllotaxis: 1. spiral, 2. opposite, 3. whorls of three, 4. verticillate. 2.
Ontogenetic sequence of leaf types: 1. flattened linear ➤ quadrangular ➤ quadran-
gular or scale, 2. flattened linear ➤ flattened linear or scale ➤ flattened linear or
scale, 3. flattened linear ➤ cladodes and scales ➤ cladodes and scales. 3. Mature
leaf types: 1. cupressoid, 2. cryptomeroid, 3. taxoid, 4. pinoid, 5. athrotaxoid, 6.
"cladodes". 4. Stomatal distribution on leaves: 1. hypostomatic, 2. amphistoma-
tic, 3. epistomatic. 5. Orientation of stomata: 1. longitudinal, 2. diverse, 3. trans-
verse. 6. Stomatal papillae: 1. absent, 2. rare, 3. numerous. 7. Number of
stomatal subsidiary cells: 4–16. 8. Cycles of stomatal subsidiary cells: 1. mono-
cyclic, 2. weakly bicyclic, 3. bicyclic, 4. weakly tricyclic. 9. Sharing of subsidiary
cells by adjacent stomatal apparatuses: 1. never, 2. occasionally, 3. often.
  10. Shoot persistence: 1. annually deciduous, 2. semi-deciduous, 3. evergreen.
11. Haploid chromosome number: 10–11. 12. Growth rings in secondary xylem:
1. indistinct, 2. distinct. 13. Cross-sectional shape of tracheids in secondary xylem:
1. squarish, 2. rounded. 14. Average radial diameter (μm) of tracheids: 11.2–33.4.
15. Longitudinal resin ducts in secondary xylem: 1. absent, 2. rare, 3. regular.
16. Longitudinal parenchyma in secondary xylem: 1. absent, 2. present. 17. Rays
per square mm of tangential surface of secondary xylem: 15–180. 18. Ray height
(cells) in secondary xylem: 1–60. 19. Ray width (cells): 1–2.
  20. Pit diameter (μm) on tangential wall of tracheids in secondary xylem: 5–21.
21. Types of crossfield pits in secondary xylem: 1. podocarpoid, 2. dacrydioid, 3.
taxodioid, 4. cupressoid, 5. glyptostroboid, 6. piceoid. 22. Number of pits in cross-
field: 1–8. 23. Ray tracheids in secondary xylem: 1. absent, 2. occasional. 24.
Horizontal walls of wood parenchyma: 1. smooth, 2. thickened or nodular. 25.
Horizontal walls of ray cells: 1. smooth, 2. coarse, 3. pitted. 26. Tangential walls
of ray cells: 1. smooth, 2. nodular. 27. Biflavonoid series: 1. amentoflavone, 2.
hinokiflavone, 3. cupressuflavone, 4. dihydrobiflavonoids. 28. Leaf wax: 1. non-
estolide, 2. estolide. 29. Tropolones: 1. absent, 2. present.
  30. Sesquiterpene series: 1. cedrane, 2. humulane, 3. thujopsane, 4. cuparane, 5.
selinane, 6. guaiane, 7. cadinane, 8. caryophyllane. 31. Glycoflavonoids: 1. absent,
2. present. 32. Arrangement of microsporangiate strobili: 1. solitary, 2. spicate,
3. aments, 4. whorled. 33. Number of microsporangia per microsporophyll: 2–10.
34. Leptoma of pollen grain: 1. smooth, 2. pouting, 3. papillate. 35. Shape of
ovuliferous cone scale: 1. peltate, 2. elongate, 3. flattened, 4. triangular. 36. Num-
ber of seed wings: 0–3. 37. Ovules per ovuliferous scale: 1–20. 38. Ovule orien-
tation: 1. erect, 2. inverted. 39. Arrangement of megaspores after meiosis: 1.
linear, 2. various, 3. T-shaped.
  40. Grouping of archegonia in megagametophyte: 1. solitary, 2. in a ring, 3. in
complexes. 41. Position of archegonia: 1. micropylar, 2. lateral. 42. Structure of
young megagametophyte: 1. single layer, 2. upper part single, lower part double
or massive, 3. double layer. 43. Archegonial jacket: 1. scattered cells, 2. single
layer, uninucleate, 3. single layer, partly binucleate, 4. multiple layers, 5. absent.
44. Number of embryonic free nuclear divisions: 0–5. 45. Number of cells in
E-tier of proembryo: 1–20. 46. Upper tier of proembryo: 1. absent, 2. open, 3.
partly closed, 4. closed. 47. Primary embryonic suspensor: 1. absent, 2. present.
48. Cleavage of polyembryony: 1. absent, 2. present. 49. Number of cotyledons:
2–9.

important reproductive and anatomical characters) between taxodia-
ceous and cupressaceous genera (Table 3), much as other coniferous
families have distinctive character assemblages. The magnitude of this

TABLE 6. CHARACTERIZATION OF CUPRESSUS, CALLITRIS, AND TAXODIACEOUS GENERA USING CHARACTERS AND THEIR STATES AS LISTED IN TABLE 5. This table was compiled using the following references in addition to personal observations: Butts and Buchholz (1940), de Laubenfels (1953; 1962), Dogra (1967), H. Erdtman and Norin (1966), Florin (1930; 1952), Gaussen (1944–1974), Geiger and Buck (1973), Geiger and de Groot-Pfleiderer (1973), Greguss (1955; 1972), Khoshoo (1961), Locksley (1972), Maheshwari and Singh (1967), Niemann and Miller (1975), Roy Chowdhury (1962), Wang and Chien (1964). Character states in parentheses are uncommon conditions or extremes. Double parentheses indicate extremely rare character states. A dash indicates inapplicability of a character to a genus.

Sciadopitys: 1:1,4; 2:3; 3:1,6; 4:1; 5:1; 6:3; 7:8; 8:1; 9:1; 10:3; 11:10; 12:2; 13:1; 14:22.4; 15:1; 16:1; 17:32–35; 18:1–7(10); 19:1; 20:8–9; 21:1,2; 22:1(2); 23:1; 24:—; 25:1; 26:1; 27:1,2; 28:1; 29:1; 30:1; 31:1; 32:2; 33:2; 34:1; 35:2; 36:2; 37:5–9; 38:2; 39:1; 40:1; 41:1; 42:1; 43:2; 44:5; 45:12–20; 46:3; 47:1; 48:2; 49:2(4).

Sequoia: 1:1; 2:2; 3:1–3; 4:2; 5:2; 6:1; 7:4–5(10); 8:3; 9:1; 10:3; 11:33; 12:(1),2; 13:1,(2); 14:29.5; 15:3; 16:2; 17:30–40; 18:1–20(30); 19:1(2); 20:14–16; 21:3,(1,4,5); 22:1–3(5); 23:2; 24:1,2; 25:1,(3); 26:1,(2); 27:1; 28:2; 29:?; 30:?; 31:2; 32:1; 33:2–5; 34:1,3; 35:1; 36:2; 37:5–7; 38:2; 39:2; 40:3; 41:2; 42:2; 43:1; 44:0; 45:4; 46:1; 47:2; 48:2; 49:2.

Sequoiadendron: 1:1; 2:1; 3:1,2; 4:2; 5:2; 6:2; 7:4–6(12); 8:3; 9:1; 10:3; 11:11; 12:2; 13:1,(2); 14:21.3; 15:3; 16:2; 17:40–45; 18:1–12(30); 19:1(2); 20:11–13; 21:3,(1,4,5); 22:1–2(6); 23:2; 24:1,2; 25:1,(3); 26:1; 271,2; 28:?; 29:?; 30:?; 31:1; 32:1; 33:(2)3(5); 34:1,3; 35:1; 36:2; 37:3–9; 38:2; 39:1; 40:3; 41:2; 42:1; 43:1; 44:3; 45:2–3; 46:3; 47:1; 48:2; 49:(2)–(6).

Metasequoia: 1:2; 2:2; 3:4; 4:2; 5:1; 6:3; 7:4–10(12); 8:2; 9:1; 10:1; 11:11; 12:2; 13:1; 14:27.8; 15:2; 16:2; 17:45–50; 18:1–16(20); 19:1(2); 20:9–10(13); 21:3,(4,5); 22:1–2(4); 23:2; 24:1?,2; 25:1–3; 26:(1),2; 27:1,2,4; 28:1; 29:?; 30:?; 31:1; 32:3; 33:(2)5–8(9); 34:1,2; 35:1; 36:2; 37:5–8; 38:2; 39:1; 40:3; 41:1,(2); 42:1; 43:2; 44:3; 45:2–4; 46:2; 47:2; 48:2; 49:2.

Cupressus: 1:2; 2:2; 3:1; 4:2; 5:1; 6:3; 7:4–6(7); 8:2; 9:3; 10:3; 11:11; 12:1,2; 13:1,(2); 14:12.1–32.0; 15:2; 16:2; 17:65–180;18:1–12(30); 19:1,((2)); 20:6–13; 21:4; 22:1–3(5); 23:1; 24:1,2; 25:3; 26:1,2; 27:1–3; 28:?; 29:2; 30:1–4; 31:1; 32:1; 33:3–10; 34:1; 35:1; 36:2; 37:3–20; 38:1; 39:1; 40:3; 41:1; 42:1; 43:2; 44:2–3; 45:2–4; 46:2; 47:2; 48:2; 49:(2)–(5).

Callitris: 1:3; 2:2; 3:1; 4:2; 5:1; 6:2; 7:4–6(10); 8:2; 9:3; 10:3; 11:11; 12:1,2; 13:(1),2; 14:11.2–33.4; 15:3; 16:2; 17:15–120; 18:1–10(25); 19:1,((2)); 20:5–21; 21:(1),4,6; 22:1–2(4); 23:1; 24:1; 25:1,((3)); 26:1; 27:2; 28:2; 29:1; 30:5,6; 31:1; 32:1,(2); 33:2–4; 34:1; 35:4; 36:1–30; 37:2–8; 38:1; 39:1; 40:3; 41:2; 42:3; 43:2; 44:2; 45:4; 46:4; 47:2; 48:2; 49:2.

Taxodium: 1:1; 2:2; 3:1,3; 4:2; 5:3; 6:1; 7:4–8(16); 8:3; 9:2; 10:1,2; 11:11; 12:(1),2; 13:1; 14: 20.9–31.6; 15:2; 16:2; 17:50–80; 18:1–24(60); 19:1,((2)); 20:8.5–11.0; 21:3,(1,4,5); 22:1–4(8); 23:1; 24:1; 25:1,3; 26:1; 27:1,2; 28:1; 29:1; 30:5; 31:1; 32:3; 33:(3)4–5(9); 34:1,2; 35:1; 36:0; 37:2; 38:1; 39:1; 40:3; 41:1; 42:1; 43:3; 44:3; 45:2–3; 46:2; 47:1; 48:2; 49:(2)–(9).

Glyptostrobus: 1:1; 2:1; 3:1–3; 4:2; 5:1; 6:1; 7:4–6(13); 8:4; 9:1; 10:2; 11:11; 12:2; 13:1; 14:21.3; 15:2; 16:2; 17:85–90; 18:1–18(30); 19:1(2); 20:10–11; 21:(3,4),5; 22:1–4; 23:1; 24:1; 25:2,3; 26:1; 27:2; 28:1; 29:?; 30:?; 31:1; 32:1; 33:2; 34:1,2; 35:2; 36:1; 37:2; 38:2; 39:1; 40:3; 41:1; 42:1; 43:?; 44:3; 45:4; 46:2; 47:1; 48:2; 49:3–4.

Cryptomeria: 1:1; 2:1; 3:2; 4:2; 5:2; 6:1; 7:4–6(12); 8:3; 9:2; 10:3; 11:11; 12:2; 13:1; 14:16.7; 15:2; 16:2; 17:40–45; 18:1–20(24); 19:1(2); 20:9–12; 21:(3,4),5; 22:1–2(5); 23:1; 24:1; 25:1,2; 26:1; 27:1,2; 28:2; 29:1; 30:5,7; 31:1; 32:2; 33:(3)–(5); 34:3; 35:2; 36:0(3); 37:2–6; 38:1; 39:1; 40:3; 41:1; 42:1; 43:4; 44:3; 45:2–3; 46:3; 47:1; 48:2; 49:(2)–(4).

TABLE 6. *Continued*

Cunninghamia: 1:1; 2:2; 3:3; 4:1,2; 5:1; 6:1; 7:4–6(9); 8:2; 9:1; 10:3; 11:11; 12:2; 13:1,(2); 14:31.8; 15:2; 16:2; 17:100–105; 18:1–7(30); 19:1(2); 20:6.5–11.0; 21:1,(3),5; 22:1–3(5); 23:1; 24:1; 25:1,(2); 26:1; 27:1,2; 28:2; 29:1; 30:1; 31:1; 32:4; 33:2–4; 34:1; 35:3; 36:2; 37:3; 38:2; 39:1; 40:2; 41:1; 42:1; 43:3; 44:3; 45:2–3; 46:2; 47:2; 48:2; 49:2.

Taiwania: 1:1; 2:1; 3:1,2; 4:2; 5:1; 6:1; 7:4–6(14); 8:4; 9:2; 10:3; 11:11; 12:2; 13:1; 14:14.3; 15:1; 16:2; 17:85–90; 18:1–7(10); 19:1; 20:7–8; 21:1,3–5; 22:1–3(7); 23:1; 24:—; 25:1; 26:1; 27:2; 28:(1),2; 29:1; 30:1,2,5,7,8; 31:1; 32:1; 33:2; 34:1; 35:3; 36:2; 37:1–2; 38:2; 39:?; 40:?; 41:?; 42:?; 43:4; 44:3; 45:2–3; 46:4; 47:1; 48:2; 49:2.

Athrotaxis: 1:1; 2:2; 3:1,5; 4:2,3; 5:2; 6:1; 7:4–7; 8:1; 9:3; 10:3; 11:11; 12:2; 13:1; 14:25.0; 15:3; 16:2; 17:50–60; 18:1–12(14); 19:1(2); 20:10–12; 21:3; 22:1?3(6); 23:1; 24:1; 25:1,(2); 26:1; 27:?; 28:?; 29:1; 30:1,7; 31:1; 32:1; 33:2(4); 34:2; 35:2; 36:2; 37:3–6; 38:2; 39:3; 40:3; 41:2; 42:2; 43:5; 44:(1)2; 45:1; 46:4; 47:1; 48:1; 49:2.

agreement is revealed by comparisons of similarity values between pairs of families (Table 4). While Podocarpaceae, Araucariaceae, Cephalotaxaceae, and Pinaceae resemble each other in 29 to 59 percent of comparisons, and while each resembles the taxodiaceous and cupressaceous genera in 36 to 52 percent of comparisons, the cupressaceous genera share 90 percent of their character states with the taxodiaceous genera. This is about the same similarity as shown by *Pinus* to other genera of Pinaceae, some aberrant podocarps and "typical" Podocarpaceae, or *Agathis* and *Araucaria*. Resemblance of cupressaceous and taxodiaceous genera is further emphasized by examination of the five characteristics in which the former exhibit character states not found in the latter. Phyllotaxis, tangential wall of ray parenchyma cells, biflavonoid series, number of ovules per ovuliferous scale, and texture of ovuliferous scale are all characters that vary among taxodiaceous genera. Distinctive states found in cupressaceous genera (whorled phyllotaxis, scalariform walls, cupressuflavone, up to twenty ovules, and fleshy cones) are generally exaggerations of taxodiaceous trends and some are confined to single genera.

Phyllotaxis. Since separation of Cupressaceae s. s. from "Taxodiaceae" has historically been based on phyllotaxis, it is important to assess the value of this character for familial delimitation. Even without reference to the decussate leaves of *Metasequoia*, or the spiral leaves of immature plants of *Widdringtonia*, one can see that phyllotaxis (Table 3) is a poor family character. Only Cephalotaxaceae and Pinaceae have uniform phyllotaxis. The former is monotypic and the latter shows variations of spiral phyllotaxis due to differential internodal elongation. Araucariaceae and Podocarpaceae have some genera with spiral leaves and other genera with opposite leaves, and *Podocarpus* s. l. has both conditions. While Cupressaceae s. s. is the sole coniferous group that has whorls of three or four leaves at a node, most cupressaceous genera have

TABLE 7. PERCENTAGE SIMILARITY OF CUPRESSUS, CALLITRIS, AND TAXODIACEOUS GENERA. Coefficients were calculated by dividing similarities by total number of comparisons (in parentheses) for each pair.

	Sciadopitys	Sequoia	Sequoiadendron	Metasequoia	Cupressus	Callitris	Taxodium	Glyptostrobus	Cryptomeria	Cunninghamia	Taiwania	Athrotaxis
Sequoia	40(58)											
Sequoiadendron	49(55)	75(59)										
Metasequoia	45(66)	62(61)	70(60)									
Cupressus	39(59)	62(55)	68(56)	72(54)								
Callitris	40(58)	68(59)	66(56)	60(58)	68(60)							
Taxodium	44(59)	50(58)	66(58)	69(58)	63(56)	56(63)						
Glyptostrobus	47(51)	56(55)	71(56)	66(53)	61(51)	55(56)	70(54)					
Cryptomeria	45(58)	53(53)	83(54)	65(57)	62(55)	58(59)	68(57)	73(52)				
Cunninghamia	51(55)	62(56)	72(54)	72(54)	64(56)	54(59)	62(56)	58(48)	62(52)			
Taiwania	50(54)	50(50)	71(49)	50(52)	43(53)	50(58)	56(55)	64(45)	63(55)	55(56)		
Athrotaxis	46(50)	63(52)	66(50)	55(51)	50(54)	52(61)	51(55)	54(46)	55(49)	56(52)	55(49)	

opposite leaves. Since the whorled condition has probably arisen independently in different lines (e.g., in *Juniperus* and the Callitroids), it is not strong evidence for familial segregation.

Leaf Form. The other major vegetative character historically used to divide taxodiaceous and cupressaceous genera into two families is leaf form (Table 3). Cupressoid and cryptomerioid scale leaves found in cupressaceous genera are also found in taxodiaceous genera, along with taxoid and pinoid leaves, among others. *Microcachrys* bears the same relation (in terms of leaf form and phyllotaxis) to the majority of Podocarpaceae that *Cupressus* does to the taxodiaceous genera. While most podocarps, like several taxodiaceous genera, have spirally arranged taxoid leaves, *Microcachrys,* like *Cupressus,* has decussate scale leaves. This has never, to my knowledge, led to a suggestion for segregation of *Microcachrys* into a separate family.

Additional Vegetative Characters. Despite variability within families and overlap between families, there is a distinctive array of vegetative features for each conifer family, including Cupressaceae s. l. Shoot organization, chromosome number, and crossfield pitting, taken together, are sufficient for distinguishing families. Cupressaceae s. l. differs from Cephalotaxaceae in phyllotaxis, from Pinaceae in abscising lateral shoot systems instead of individual leaves, from Araucariaceae and Podocarpaceae in crossfield pit-types, and from all except Podocarpaceae in chromosome number. Other character states are features of this family alone (L-shaped branching, scalariform walls of ray parenchyma cells) or are shared with some but not all other families (ontogenetic sequence of leaf types).

Reproductive Characters. In characters of microsporangiate structures (orientation and number of microsporangia on microsporophyll, microlept spheroidal pollen grains) and male gametophytes (taxodian development), taxodiaceous and cupressaceous genera show complete agreement and contrast with all families except Cephalotaxaceae, which differs (in male characters) only in having unequal male gametes. Megasporangiate characters (complete fusion of ovuliferous scale with bract, number of ovules per ovuliferous scale and their occasional erect orientation) and megagametophytic characters (archegonial complexes sometimes lateral, no more than four neck cells in archegonium) also show close overall agreement, though taxodiaceous genera tend to be more diverse than genera in other families. Archegonial complexes and structure of ovulate cone are characteristic of Cupressaceae s. l. and such cupressaceous specializations as the fleshy "berry" of *Juniperus* (associated with bird dispersal) or the relatively large number of ovules on cone scales of certain *Cupressus* species are no more unusual among taxodiaceous genera than the disintegrating cone and large seeds of *Taxodium,* which adapt it for water dispersal. The general ground plan of embryogeny (relatively few free nuclear divisions, prosuspensor, primary and secondary suspensors, and cleavage polyembryony all present) is also characteristic of Cupressaceae s. l. Such unusual features as

accessory embryos derived from the E-tier and diamond-shaped embryos are found only in taxodiaceous and cupressaceous genera.

Taxodiaceous genera are more diverse in most of these features than cupressaceous genera and this diversity includes most character states found in the latter. Cupressaceae s. l. is little more diverse than "Taxodiaceae" and is comparable in diversity to the other large families Pinaceae and Podocarpaceae. If only two or three cupressaceous genera were known, rather than eighteen, they would likely never have been separated from the taxodiaceous genera in a segregate family.

Similarities within Cupressaceae s. l.

Since cupressaceous genera are too numerous to treat all in detail here, I have chosen *Cupressus* and *Callitris* as relatively primitive representatives of the two cupressaceous subtribes (Table 1) to compare with the taxodiaceous genera in a manner analogous to the comparison of conifer families. Many characters compared for these genera (Table 5) are the same as those compared for families (Table 2), but many additional features, such as epidermal characters, are used and several features without diagnostic value within Cupressaceae (such as ectotrophic mycorrhizae, fibrous bark, presence of both sequoyitol and pinitol, and taxodian development of microgametophyte) are deleted. Character profiles for the genera (Table 6) show considerable diversity in such characters as leaf form, density of rays in secondary xylem, sesquiterpene series, and structure of megagametophyte. The most distinctive profile belongs to *Sciadopitys*, which, with its unique "cladodes", chromosome number, and other features, is morphologically isolated within Cupressaceae. The average of similarity values in comparisons of *Sciadopitys* with other genera of Cupressaceae (Table 7) is 45 percent compared with an average of 61 percent for comparisons of genera within Cupressoideae, a difference significant at $P < 0.001$. This supports its assignment to a monotypic subfamily and provides a rationale for omitting it from discussion of affinities of other genera.

Genera of Cupressoideae compared here (Table 7) seem about equally similar to each other, with values ranging mostly from 50 to 75 percent (av. 61 percent, s. d. 8.09). Genera of Cupresseae form a closely knit group with average similarity 65 percent for comparisons within the group, contrasted with 60 percent average similarity for comparisons of these genera with other genera of Cupressoideae (different at $P < 0.05$). Genera of Cunninghamieae form a much looser aggregation having an average similarity of only 55 percent with each other (different at $P < 0.05$ from the average value for comparisons within Cupresseae). Within Cupresseae, *Cupressus* has about the same high similarity to *Metasequoia* and *Sequoiadendron* as it does to *Callitris*, while the latter is as similar to *Sequoia* and *Sequoiadendron* as it is to *Cupressus* (all about 70 percent). The alignment of these cupressaceous genera with other Cupresseae is underlined by their

average similarity of 64 percent to taxodiaceous genera of this tribe, which is significantly different at P < 0.01 from their average similarity of 54 percent to other taxodiaceous genera.

Cupressus and *Callitris,* separately, seem to fit rather well in Cupresseae. *Cupressus* in particular, with its globular ovulate cones and peltate cone scales (Table 6), seems a close relative of *Sequoia, Sequoia-dendron,* and *Metasequoia. Callitris,* while differing in these features from other Cupresseae discussed, agrees with the sequoiids in such characters as lateral archegonia and presence of stomatal papillae. *Cupressus* and *Callitris* agree in some other features common to the majority of cupressaceous genera, such as whorled phyllotaxis in seedlings, but a similar phyllotaxis occurs sporadically in taxodiaceous genera (de Laubenfels, 1953). Furthermore the two genera differ, among other characters, in the absence of tropolones in *Callitris* and in the peculiar embryogeny of the latter, which is shared with *Athrotaxis* among taxodiaceous genera (Table 6). De Laubenfels (1965) has already pointed out the taxodiaceous character of *Cupressus* on the basis of a dozen characters compared for a few taxodiaceous genera. He concluded that *Cupressus* was about equally related to *Sequoiadendron* and *Crypto-meria* (a conclusion not supported here) but he did not draw the conclusion that the cupressaceous and taxodiaceous genera should be united in a single family, despite his assertion of multiple interrelationships between them. Since *Cupressus* and *Callitris* have the same degree of similarity to the taxodiaceous genera as the latter have to each other, segregation of the cupressaceous genera as a separate family would require fragmentation of the taxodiaceous genera into several families (in the manner of Hayata, 1931; 1932) to achieve a consistent system. I prefer the alternative course of treating all as members of a single family.

Evolutionary Relationships

Fossilized remains of Cupressaceae s. l. are abundant and widespread in Mesozoic and Tertiary sediments (Florin, 1963) but taxonomy of these remains is as yet unsatisfactory. There have been a few revisions of small groups (Chaney, 1951) or for limited geographical areas (Schweitzer, 1974), but there has been no comprehensive monograph of the family, and much of the paleobotanical literature is by authors unfamiliar with the morphological range of living taxa. Since relatively few fossilized reproductive structures referable to this family are known, most records of occurrence are based on the relatively undiagnostic fragments of vegetative shoots. No adequate taxonomic framework for fossil members of this family exists and many reports of their occurrence give inadequate attention to morphological features of the remains. Thus any discussion of evolutionary relationships within Cupressaceae must be somewhat speculative. Nonetheless, careful comparisons among extant taxa and attention to some reliable fossil representatives give clues to the evolutionary trends within the family.

Specializations of cupressaceous genera of the northern hemisphere all seem derivable from an ancestral condition of globular, many-scaled ovuliferous cones, cruciate, terete branchlets, and arborescent habit. These characteristics are present in certain living species of *Cupressus* and this genus is thus similar to the probable ancestor of other genera of Cupresseae subtribe 3. Morphological features of cupressaceous genera of the southern hemisphere do not point so directly to *Cupressus* as an ancestral type. A lineage involving *Widdringtonia, Tetraclinis, Libocedrus,* and *Austrocedrus* could have originated initially from a *Cupressus*-like form by reduction to two pairs of ovuliferous cone scales, but the *Callitris-Actinostrobus-Neocallitropsis* lineage resists a similar interpretation. *Austrocedrus* and *Libocedrus,* furthermore, could be allied to the northern hemisphere *Calocedrus,* which has been considered congeneric with them (Janchen, 1950), rather than to *Widdringtonia* and *Tetraclinis.* The exact placement of these two genera must await further morphological and embryological observations, but their morphology is closely comparable to that of other cupressaceous genera. In fact, genera of Cupresseae subtribes 3 and 4 are an assemblage of diversified descendants of relatively recent ancestors, while the taxodiaceous genera mostly represent remnants of lineages, equivalent to, but smaller than, these cupressaceous lines. Relative success of cupressaceous lines can be related in part to their vegetative morphology. Their diversification may have resulted from their evolution of xeromorphic scale leaves, which allowed them to survive the increasing aridity of the Tertiary (Wolfe, 1969) better than the other, broader-leaved taxodiaceous forms. The three largest cupressaceous genera (*Cupressus, Callitris,* and *Juniperus*), which are still in a state of evolutionary diversification (as evidenced by intergradation and hybridization), have cupressoid scale leaves in most or all species. Significantly, those cupressaceous genera that have broader leaves (e.g., *Thuja, Libocedrus,* and *Fitzroya*) are morphologically specialized genera (Li, 1953a) whose secondary invasion of more mesic habitats has been associated with a re-expansion of leaf surfaces. These derivative genera have retained the phyllotactic patterns of their scale-leaved ancestors.

Scale leaves are not invariably associated with decussate or whorled leaf arrangements. All shoots of *Athrotaxis cupressoides* and mature leading shoots of other extant taxodiaceous species have spirally arranged scale leaves. Furthermore, shoots of several extinct taxodiaceous forms (some species of *Brachyphyllum, Thuites,* and *Cyparissidium*), extending back to the Jurassic (Florin, 1963), also have this arrangement. The oldest known conifer remains with decussate scale leaves are referred to *Cupressinocladus ramonensis* (Chaloner and Lorch, 1966) from the Jurassic of Israel. While the authors consider this a cupressaceous form, its reproductive structures are as yet unknown, and its stomatal characters are also shared with taxodiaceous genera. A reasonable interpretation of these facts is that various taxodiaceous lines have

experimented with either scale leaves or decussate (or whorled) phyllotaxis, or both. Two (or three) of these lines, the cupressaceous forms, have been successful and have continued and expanded to the present, while other lines became extinct or have barely persisted (e. g., *Metasequoia*).

Despite their present restricted distributions, several taxodiaceous genera of Cupresseae were much more widespread during the Tertiary (Chaney, 1951; Florin, 1963) but they never underwent adaptive radiations comparable to those of the callitroid and cupressoid lines. While some taxodiaceous and cupressaceous genera were present in the Cretaceous or earlier, most seem to have emerged in the early Tertiary and are comparable in age to many angiosperm tree genera. As a result of a probable rapid adaptive radiation of callitroid and cupressoid lines in the Upper Cretaceous and Paleogene, many of the derivative genera (such as *Thuja* and *Chamaecyparis*) coexisted with relatively unmodified taxodiaceous genera throughout much of the Tertiary. The deceptive antiquity of the cupressoid derivatives is partly an artifact of the relatively poor record of Jurassic and Cretaceous conifers everywhere except in Europe, which is probably not the center of evolution of Cupressaceae. Thus we know very little about the emergence of taxodiaceous genera, since their first records are quite similar to living taxa and do not point to their ancestry. Until we have much more Mesozoic evidence, especially of reproductive structures, we cannot more closely trace evolutionary patterns within Cupressaceae. Nothing in current paleobotanical literature, however, contradicts the notion that taxodiaceous and cupressaceous genera are members of the same family.

Taxonomic Conclusions

Since *Cupressus* and *Callitris* are as closely allied to *Sequoia, Sequoiadendron,* and *Metasequoia* as the latter are to other taxodiaceous genera, the usual assignment of the first two genera to one family and the latter three to another is phylogenetically and taxonomically unacceptable. Considering the pattern of similarities that the genera display, there seem to be two possible courses available that would result in their consistent treatment. The first would be to follow Hayata (1931, 1932) in recognizing a large number of small families that are equivalent in rank to Cupressaceae s. s. The second is to treat all the genera (with the possible exception of *Sciadopitys*, which could reasonably be assigned to a monotypic family) as members of a single family. I prefer to preserve indications of relationship within the taxonomic system. Current practice in circumscription of other conifer families also favors the conservative approach. Cupressaceae, as circumscribed here, is equivalent in diversity to Pinaceae or Podocarpaceae.

Since this is not a detailed taxonomic revision of Cupressaceae, the proposed arrangement of genera (Table 1) must be tentative. While relationships of certain genera (*Cryptomeria, Athrotaxis, Tetraclinis,*

and some other callitroid genera) are problematical, this scheme is consistent with available evidence of relationships and provides a basis for further discussion of this group of conifers.

Acknowledgments

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